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THE IMPLICATIONS OF PHYLOGENETIC ANALYSIS FOR COMPARATIVE BIOLOGY: THE THIRTIETH ANNUAL SYSTEMATICS SYMPOSIUM

This symposium brings together seven systematic biologists to discuss the relationship between phylogenetic systematics (cladistics) and various branches of comparative biology. Cladistic theory and method were not the focus of this symposium, but rather it addressed how the results of cladistics—that is, hypotheses about phylogenetic pattern—are an essential component of historical analysis. Thus, the papers presented here illustrate six specific problems that, directly or indirectly, rely on cladistic analysis for their solution.

Cladistics became an important force within systematic biology following the English translation of Willi Hennig's "Grundzuge einer Theorie der phylogenetischen Systematik" (1950), which was updated in 1966 as "Phylogenetic Systematics." From that time, cladistics has steadily increased in influence, first within zoology, and somewhat later in botany (for an introduction to cladistics, see Eldredge & Cracraft, 1980; Wiley, 1980, 1981; Patterson, 1980; Nelson & Platnick, 1981; Cracraft, 1983; Humphries & Funk, 1984). During this period many workers have discussed the pros and cons of cladistics, and frequent misunderstandings about the theoretical and methodological content of cladistics have arisen. Perhaps contributing to this situation is the fact that the views of cladistic theoreticians have also evolved, often along divergent pathways so that the field of cladistics is now broader, and consequently more internally contentious, than it was 15 years ago. Despite this diversity, the question can be asked whether cladistics is united by any underlying principles so as to form a coherent

research program. An answer to this question is of interest beyond being able to differentiate cladists or their work, because it also helps to place the various transformations of cladistics into a common framework and to gain a perspective on some of the arguments that are currently being expressed over the meaning and content of cladistic thought.

THE PRINCIPLES OF CLADISTICS

We do not wish to engage in an extended discussion of the historical changes that have taken place in the thinking of individual cladists. We want, instead, to call attention to a common intellectual thread that has passed through the writings of cladists from Hennig to the present. We perceive this thread to consist of two principles: (1) taxa are united into natural groups on the basis of shared derived characters, or synapomorphies (the Principle of Synapomorphy), and (2) classifications must express those taxic patterns of synapomorphy explicitly (the Principle of Strict Monophyly). To be sure, each of these principles may rely on certain unexpressed assumptions, but none we think that are not also shared with noncladistic methods of systematics. For instance, Platnick's (1979: 538) first principle of cladistics, that nature has a single historical pattern with a hierarchical structure, would probably be acceptable to the majority of systematists.

With respect to these two principles, the Principle of Synapomorphy is clearly primary in that the Principle of Strict Monophyly depends on it.

Pheneticists and their followers reject the first principle, and therefore, logically also reject the Principle of Strict Monophyly. Some evolutionary (or eclectic) systematists might well accept the Principle of Synapomorphy but advocate paraphyletic taxa, thereby rejecting the Principle of Strict Monophyly; in fact, however, we believe that most evolutionary systematists, like pheneticists, reject both principles.

We also suggest that a third principle has been central to cladistic theory and methodology, namely, the Principle of Strict Parsimony. Although an acceptance of parsimony is basic to all scientific reasoning, cladists have certainly been much more concerned with elucidating the relationship of parsimony to systematics and applying parsimony analysis to their work than have advocates of phenetics or evolutionary systematics. Some of the critical literature discussing the application of parsimony to systematic hypotheses includes Kluge and Farris (1969); Gaffney (1979); Farris (1982, 1983), Sober (1983a, 1983b), and Maddison et al. (1984).

Within a cladistic framework taxa are grouped on the basis of shared character transformations. All such characters are termed synapomorphies. Some of these transformations will be unique, others may have arisen more than once within the group being studied and may be termed homoplasious. Obtaining a final interpretation of the pattern of the character transformation for any specific character depends on the tree topology (phylogenetic hypothesis) upon which all character transformations are optimized. Thus, we choose that tree by maximizing the congruence of character transformations across the *entire* data set. Logically, this also implies that homoplasies are minimized, thus resulting in the fewest *ad hoc* hypotheses required to explain those character distributions (Wiley, 1975; Farris 1982, 1983). Within this methodological framework, it is clear that homoplasies (parallelisms, convergences, reversals) are also synapomorphies: they represent derived character transformations defining two or more unrelated groups of taxa ("unique" synapomorphies define only a single group).

The Principle of Strict Parsimony has been a core methodological component of mainstream cladistics for nearly two decades. In recent years, a small number of workers, also claiming to practice cladistics, have advocated abandoning (or at least relaxing) this principle in favor of a method that constructs trees using only a subset of the

original character data. This method, called compatibility or clique analysis, unites taxa by utilizing those characters that exhibit congruence and eliminating those showing homoplasy (Estabrook et al., 1976; Meacham, 1984). Compatibility methods have been strongly criticized from several standpoints (Farris & Kluge, 1979; Mickevich & Parenti, 1980; Churchill et al., 1984). We note here the primary philosophical objection: a given scientific hypothesis, including those within systematics, has veracity compared to competing hypotheses when it best explains all of the relevant data, thus it is unclear to what extent hypotheses can be objectively compared when we exclude from consideration data that might be incongruent with one or more of the alternatives.

THE CHANGING FACE OF CLADISTICS

Cladistics emerged as a solution to a long-standing problem within systematic biology: how do we come to have knowledge about the phylogenetic relationships of organisms? Most contemporary systematists employing cladistic methods still see this as the central focus of their research. For all these workers, branching diagrams (cladograms) are interpretable as phylogenetic hypotheses and represent evolutionary history. Within this framework, synapomorphies are taken to be evolutionary transformations or derivations from more primitive conditions.

The preceding describes a view of cladistics sometimes termed "phylogenetic" or "evolutionary" cladistics. To most of its practitioners, an evolutionary process underlies the rationale for the method. A claim for a specific evolutionary process is generally not made, but without the assumption of evolution, we are sometimes told, cladistics is set adrift in a sea of "conceptual confusion" (Beatty, 1982: 33). Thus, according to Wiley (1981: 22), "the formalism of taxonomy must be subservient to the demands of evolution."

An alternative viewpoint about the relationship between cladistic analysis and evolutionary theory has surfaced within the last five years. Unfortunately, it has generated substantial misunderstanding, particularly outside the cladistic community, and consequently is worthy of a few words of clarification. More or less simultaneously, a number of workers proposed that there could be a separation between reconstructing historical pattern on the one hand and assumptions

about the process underlying that pattern on the other. These systematists suggested that the analysis of systematic pattern was (or certainly could be) independent of any preconceived notion of process (Gaffney, 1979; Eldredge, 1979; Platnick, 1979; Eldredge & Cracraft, 1980; Patterson, 1980, 1982a; Nelson & Platnick, 1981).

The reaction to transformed or pattern cladistics, as the above view has been called, has run from quiet acceptance to outright hostility. Most of the latter has originated outside cladistics itself (Beatty, 1982; Ridley, 1983) and has been founded more on its misunderstandings of cladistics than on any cogent criticism of pattern cladism (see responses of Platnick, 1982; Patterson, 1982b; Brady, 1982). Nevertheless, some potentially interesting issues are being raised by cladists themselves. For example, if a specific notion of evolutionary process is unnecessary, where does that leave our interpretation of the concept of synapomorphy? Phylogenetic cladists continue to view character transformation in terms of "primitive to derived sequences" and to argue that in constructing hypotheses of this transformation we must have some prior conception of historical relationships in order to undertake outgroup analysis. Pattern cladists might respond that synapomorphy is strictly a problem of deciding the level of generality of defining characters and that this can be arrived at by inspection and comparison of ontogenetic histories, thus eliminating the need for prior phylogenetic assumptions (see Nelson & Platnick, 1981; Rosen, 1984). The issue of which method of comparison (outgroup or ontogenetic) is primary, is an empirical matter to be decided by parsimony analysis, and indeed this is being debated at this time (Kluge, 1985; Brooks & Wiley, 1985; Nelson, 1985; Platnick, 1985). Matters of principle aside, in practice cladists from either side of the debate will use both ontogenetic and outgroup data to resolve systematic relationships, so perhaps in that regard the debate will not concern those systematists interested solely in cladistics as a methodological tool.

Although cladists might differ in their perceptions about the role of evolutionary assumptions within cladistics, as we noted earlier a shared set of common principles can be identified. To our knowledge, all pattern cladists believe in naturalism, whereby the hierarchical pattern of nature is assumed to be the result of naturalistic processes. Thus, to claim that pattern cladists do not believe in some form of "evolutionary" (his-

torical) process behind phylogenetic pattern or that pattern cladistics is "antievolutionary" is simply mistaken. Pattern cladists merely claim that a prior commitment to a specific process is unnecessary in order to generate hypotheses about that pattern. And given that hypotheses about pattern have been proposed for hundreds of years, under different theoretical paradigms about the causes of that pattern (Patterson, 1977; Nelson & Platnick, 1981), their point seems to be well taken.

THE SYMPOSIUM

Speciation analysis. In the first paper, E. O. Wiley and R. L. Mayden show how the results of a cladistic study can be used to examine patterns and processes of speciation. Using species-level taxa within the eastern North American fish fauna, they begin by briefly discussing attitudes towards species concepts as they have been used by phylogenetic systematists. Wiley and Mayden then investigate patterns of relationships for numerous clades of fishes having common species borders of endemism. They show that these historical hypotheses inhibit intercladal congruence, which they then use as components of an analysis of speciation modes.

Historical biogeography. Donn Rosen begins his paper by addressing two widely held, but incorrect, assumptions: that fossils can tell us how old a taxon is, and that the ages of geologic events have been correctly assigned. He emphasizes the need for precision in specifying how historical biology is related to historical geology and shows how cladistics permits comparisons between these two systems. He seeks to discover patterns of congruence between historical biogeography and geological events so explicit that the congruence discovered cannot be dismissed as being due to chance or coincidence. Rosen stresses that it is the "independence of biological from geological data that makes the comparison of the two so interesting" He reviews Caribbean geologic history and presents a cladistic hypothesis for the historical interrelationships of the areas of that region. He points out that complex histories should lead us to expect complex patterns and that all potential hypotheses of area relationships may be corroborated by one or more cladistic patterns exhibited by the endemic taxa. Rosen also raises a warning for biogeographic analysis: in the past, some workers have assumed that dispersal is demonstrated by failure to discover

congruence in area relationships, yet even though dispersal may be widespread "theories of dispersal to explain biotic complexity are no more informative than theories of relationship based on symplesiomorphy"

Historical ecology and coevolution. Daniel Brooks discusses analytic methods of historical ecology and shows how they provide a missing component in studies analyzing the evolution of ecological associations. Direct estimates of ecological history are obtained by constructing cladistic hypotheses for as many interacting groups of organisms as possible. This method is contrasted with evolutionary ecology, which often uses indirect estimates such as the assumption that the age of ecological associations is proportional to its diversity. Using host-parasite data, Brooks addresses three questions within historical ecology: (1) How did species occurring in a given area come to be assembled? (2) How did two or more species having a close and evident ecological relationship come to be that way? And (3) Under what conditions did the ecological life history traits that we observe today emerge? Brooks shows how historical analysis through cladistics can provide insights into all of these ecological questions.

Hybridization. Vicki Funk addresses one of the major concerns of plant systematists, namely how to analyze hybridization within the context of a phylogenetic hypothesis. She summarizes the problems that arise during a cladistic analysis of a group whose taxa hybridize with one another, and she presents guidelines for interpolating hybrids into a cladogram. In order to exemplify these methods, she undertakes cladistic analyses of seven different genera exhibiting various degrees of hybridization among their component taxa. Funk stresses that all hypotheses regarding hybrid identification must be corroborated by chromosomal, distributional, and ecological data. A major conclusion is that cladistic analysis is indispensable when analyzing hybridization, but in cases of taxa exhibiting extensive hybridization, all systematic methods, including cladistics, may fail to give a clear indication of the history of the group.

Origin of the angiosperms. In the next paper, Peter Crane applies cladistic methodology to the question of the origin of the angiosperms. His central goal is to delineate the major groups of seed plants, to determine their interrelationships, and finally, to establish to which group of gymnosperms the flowering plants are most closely

related. Crane accomplishes this task by providing an exhaustive analysis of extant and fossil groups of seed plants and establishes a framework within which competing theories of relationships are compared. By formulating the relevant phylogenetic questions more explicitly, he also provides an alternative to the established tradition of searching for ancestral groups.

Biological diversification theory. In the final paper, Joel Cracraft briefly describes the patterns of diversification that fall within the umbrella of a general theory of diversification. He proposes a hypothesis in which speciation rates are a function of the rate of change in large-scale geomorphological complexity, whereas extinction rates are a function of temporal and spatial changes in environmental harshness. Together, these two rate-controls describe a diversity-independent process of diversification. He then summarizes some of the evidence supporting this hypothesis, pointing out that the data themselves are often dependent upon knowledge of the phylogenetic relationships of many groups of organisms.

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- Vicki A. Funk, Department of Botany, Smithsonian Institution, Washington, D.C. 20560; and Joel Cracraft, Department of Anatomy, University of Illinois, Chicago, Illinois 60680.